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## THE NATURE OF THE ABSORPTION AND TOLERANCE OF PLANTS IN BOGS<sup>1</sup>

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The consideration of measured physical habitat conditions,<sup>2</sup> which is desired as a basis for distributional relationships of plant associations, their succession and morphological distinction, and particularly for a theory of physiologically arid habitats, has not rendered clearer the nature of the absorption of plants in bogs and peat deposits. Interest in the study of the absorption and the varying degree of tolerance and resistance of plants growing in Ohio bogs has been coincident with the determination of the quantitative nature of the habitat factors, but it has been only through an appreciation of the subordinate value of the physical habitat factors that attention could be given to the special diosmotic properties of the plants and of the substances absorbed, together with the changes which the penetrating substances produce upon the plants. The changes which the substances undergo internally or externally to the absorbing cell or organ are relationships of equal importance in the problem of nutritive metabolism, but a discussion of them cannot be attempted as yet.

The evidence as to the rôle of physical and biotic habitat factors, derived from study of bog vegetation in its relations to the substratum, temperature, and evaporation, from consideration of the relation of bog vegetation to the chemical nature of peat soils,<sup>3</sup> need not be reviewed here in detail. It pointed to something else than merely the atmospheric influences as ecological conditions for the development of bogs and for the selection and growth of plants tenanting such areas.

<sup>1</sup> Contribution from the Botanical Laboratory, Ohio State University. No. 71. Read before the Botanical Society of America at the Washington meeting, 1911.

<sup>2</sup> DACHNOWSKI, A., The vegetation of Cranberry Island (Ohio) and its relations to substratum, temperature, and evaporation. *BOT. GAZ.* 52:1-33, 126-150. 1911.

<sup>3</sup> ———, The relation of Ohio bog vegetation to the chemical nature of peat soils. *Bull. Torr. Bot. Club* 39:53-62. 1912.

The evaporation in a bog forest averages 8.1 cc. daily and shows a close correspondence to the record obtained by others for a beech-maple forest.<sup>4</sup> In a bog meadow the rate (10.9 cc. daily) is less than that for the open campus of the State University (15.8 cc. daily). As far as local atmospheric conditions are concerned, the rate of evaporation is not a sufficient cause to determine succession of vegetation, nor are the differences in the rates efficient limiting factors.

The rôle of substratum temperature is obviously not the most direct factor in southern localities contributing to the causal relation between water requirements of bog plants and available supply. Neither has the coefficient of the differences between soil and air temperatures a greater value in the selection of plants for bog areas, or in their root functions.

The concentration of mineral salts in bog water from various plant associations ranges between 40 and 160 parts per million; the acidity of the solutions varies from less than 0.00075 to 0.004 normal acid, when titrated with NaOH. There seem to be no free "humus" acids. The acid reaction noted can be attributed to adsorption phenomena,<sup>5</sup> especially to the selective absorbent power of the cell colloids of disintegrating plant tissue which retain, as BAUMANN and GULLY<sup>6</sup> have shown, chiefly the basic ions of dissolved salts. The osmotic pressure of the solutions in the various associations is very nearly alike in the several plant zones and about the same as that of lake and river water. The differences cannot be associated with factors limiting the distributional relationships and the activity of plants in bogs.

Variations in the position of the water table do not influence the character of the vegetation, nor do they offer an explanation of the xerophytic structure of the plants, for the peat mat upon which the more typical bog xerophytes and heath associations succeed one another is more often a floating mat and moves with any change

<sup>4</sup> TRANSEAU, E. N., The relation of plant societies to evaporation. *BOT. GAZ.* 45: 217-231. 1908.

FULLER, G. S., Evaporation and plant succession. *BOT. GAZ.* 52: 193-208. 1911.

<sup>5</sup> CAMERON, F. K., The soil solution. 1911. p. 55.

<sup>6</sup> BAUMANN, A., und GULLY, E., Über die freien Humussäuren des Hochmoores. *Mitt. K. Bayr. Moorkulturanst.* 1910. pp. 31-56.

in the water table of the lake. In such a mat differences in the rate of the movement of water through peat soil do not exist, and hence are out of the question in the problem of the supply and the rate of removal of water by plants.

The chemical analyses of Ohio peat soils, the data of which appear elsewhere,<sup>7</sup> show wide variations, but there is a certain uniformity in the range. When a correlation between the chemical character of peat and the respective bog vegetation unit is attempted the well defined relations are these:

In poorly decomposed bog meadow peat the percentage of volatile matter is high, the percentage of fixed carbon, nitrogen, and ash is low; the reverse is true for the well decayed peat supporting a bog forest and deciduous trees.

Peat soils from various plant associations in bogs contain the essential mineral salts such as potash, phosphoric acid, and others, in inconsiderable quantities—only a fraction of 1 per cent. The salts, it seems, play only a minor rôle for protoplasmic activities, and in the growth and ripening of bog plants. Tolerance and resistance of plants to bog habitat is not an osmotic relation; it cannot be related to a greater resistance to water absorption produced by high external osmotic pressure, nor, it seems, to the lack of some one salt in the mineral content of the soil or in the plants. The ash content of the wood of bog trees is less than 0.5 per cent, with an occasional maximum of about 1.5 per cent.

The solubility of the coarsely fibrous peat from bog meadows is less than that of peat in more advanced stages of decomposition supporting genetically higher associations of plants. The quantity of nitrites, nitrates, and ammonia is very small and yet amply sufficient to support luxuriant growth. Practically all the substances in solution are transition products of proteins and carbohydrates arising through the action of obligate microorganisms. Bacteriological investigations have shown clearly the importance of biological processes. As a source of food to the microorganisms and in the nature of the organic compounds produced during the partial digestion of the upper layer of the vegetable débris, the substratum constitutes an efficient limiting and selective factor.

<sup>7</sup> DACHNOWSKI, A., The peat deposits of Ohio. Geol. Surv. Ohio, Bull. 16, 1912 (in press).

Now that it has been possible to show the inadequacy of various of the physical environmental relations of plants in bogs to account for the failure of some of the agricultural plants to thrive and for the survival of others; and since differences in light-intensity, in special absorptive powers of roots for peaty substrata, in fungal mycorrhiza, and in morphological limitations in the absorption and in the conduction of water do not enter into the problem with the agricultural plants used for the test experiments, it seems timely to consider in more detail the specific rôle of the organic decomposition products in the relation between the required quantity of available water and the quantity absorbed by the plants.

That some sort of regulatory, reciprocal mechanism, acting within certain limits, is of the utmost importance in these species seems evident from the fact that while the presence of structural modifications is generally regarded as reaction in favor of a bog vegetation, the most noteworthy characteristic which enables invading plants to resist the unfavorable conditions is a greater elasticity of functions and perhaps some specific place function. What is the mechanism connected with the failure of many agricultural plants to thrive in peat soils and in solutions of bog water? What critical features, either as products of habitat or congenital variation, do the surviving plants possess to regulate or control the absorption of injurious organic bodies, and what are the pathological aspects which involve dwarfing, leaf-fall, and general senescence in most invading species alien to the habitat?

A knowledge of the limits of functional variation within a known species and its several varieties should prove very essential as to the rôle and the range of the individual and genetic differences in the plants themselves, and the ability of the plants to inhibit the absorption of deleterious bodies, or to neutralize the injurious action of the substratum.

In the present preliminary paper data are submitted which were obtained from experiments in the laboratory with several standard varieties of grain sorghums, alfalfa, and bean. The seeds were obtained from the United States Department of Agriculture through the office of seed distribution. The seeds were germinated in sterilized quartz sand and employed in a manner

described in earlier papers. The physiological tests were made in bog water from the central (cranberry-sphagnum) station on Cranberry Island at Buckeye Lake, Ohio. All experiments were made in duplicate series. Paper-covered "Mason" jars were used containing 500 cc. of untreated bog water. The following selected series in tables I to III is especially suggestive and typical.

The tables show at a glance which of the varieties is the more efficient in counteracting the effects of injurious organic compounds. Not only the relative transpiration quantities but also the morphological effects as shown by the general appearance of roots and leaves bear out the observation that the rate of entrance of water is as high and higher than the transpiration rate. The evaporating power of the air during several of the experiments was relatively high.

Especially in bog water of greater toxicity than that of the date in the above series, the plants were in strong contrast to each other. The rate of growth varied considerably according to the amount of transpiration and to the supply of available water. The decreased permeability of the plasmatic membrane of the root-hair cells favored their efficiency in selective absorption and in growth. When the rate of transpiration decreased, the root tips and the tops made but slight growth. The roots were discolored for some distance from the tip, appeared gelatinous, and not only their surface but the meristematic tissue seemed injured, inhibiting the formation of new laterals. The leaves were short and unfolded imperfectly. At the beginning of the experiment the roots of the stronger plants were able to counterbalance the injurious action to a slight extent; light brown insoluble bodies appeared deposited upon the surface of the roots. In dilute solutions of bog water the roots remained white. Invariably, however, the toxicity was lessened most in plants whose ability to counteract the harmful effects was most pronounced. The plants functioned less readily, and their rate of reaction diminished as the active mass of bacterial products increased.

A characteristic behavior became evident in the increase of green weight of the plants in the dilute solutions, and in the observation that this effect was far from being uniform in all the cultures. The

deleterious action of bog water was, on the whole, less marked upon the tops than upon the roots. Nevertheless the green weight of some of the plants with a lower transpiration value was greater than that of the plants transpiring more strongly. Examples are numbers 3, 5, and 7 in table I; 2 and 5 in table II; 4 and 6 in table III; 7 and 10 in table IV.

TABLE I

TRANSPIRATION DATA OF VARIETIES OF GRAIN SORGHUMS<sup>8</sup> IN BOG WATER  
MARCH 6-24, 1910

Variety of sorghum	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. Milo.....	106.15	2.59	40.95
2. White Durra.....	91.05	2.18	42.98
3. Dwarf Milo.....	86.70	2.87	30.17
4. Dagdi Durra.....	78.95	1.89	41.70
5. White Kowliang.....	78.32	2.92	26.08
6. Blackhull Kaffir.....	69.95	1.40	49.85
7. Brown Kowliang.....	55.65	1.46	37.98
8. Red Kaffir.....	52.90	1.28	41.34

Atmometer: 25 cc. daily average

TABLE II

TRANSPIRATION DATA OF VARIETIES OF ALFALFA IN BOG WATER  
MAY 6-26, 1910

Variety of alfalfa	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. Medicago falcata.....	11.50	1.48	7.77
2. Var. 16399 (Washington)....	11.86	2.28	5.20
3. Var. 23625.....	8.72	0.99	8.80
4. Var. 9359 (Turkestan).....	7.32	0.59	12.40
5. Sand Lucerne 20457.....	11.93	2.21	5.40

Atmometer: 18.9 cc. daily average

It is quite generally known that rapid growth is usually accompanied by active respiration, and hence slowly developing plants are able to increase in dry weight upon a smaller quantity of water absorbed and transpired. It seems clear from the normal appearance of the roots of these plants, that the injurious substances have an entirely different effect upon some varieties of the plants with

<sup>8</sup> BALL, C. R., The history and distribution of sorghum. U.S. Dept. of Agriculture, Bur. Plant Industry, Bull. 175, 1910.

the smaller transpiration value from that observed in others. The marked difference is undoubtedly due to the nutritive value of the assimilable organic compounds. This particular feature of variability in nutritive metabolism is so characteristic and strik-

TABLE III

TRANSPIRATION DATA OF SPECIES AND VARIETIES OF BEANS IN BOG WATER  
FEBRUARY 24—MARCH 11, 1910

Species and varieties	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. <i>Dolichos</i> 22025.....	150.68	3.75	40.18
2. <i>Dolichos</i> 8542.....	99.54	1.52	65.61
3. <i>Phaseolus mungo</i> var. 18310.	66.46	1.34	49.59
4. Var. 17096.....	69.98	2.32	30.16
5. <i>Phaseolus mungo</i> .....	56.35	1.24	45.32
6. <i>Guar</i> .....	36.57	1.21	32.23

Atmometer: 7.3 cc. daily average

TABLE IV

TRANSPIRATION DATA OF WHEAT PLANTS IN SOLUTIONS OF STERILIZED BOG WATER  
AND PEAT, INOCULATED WITH BOG BACTERIA  
MARCH 31—APRIL 15, 1910

Culture	Transpiration in grams	Green weight produced	Water required for 1 gram of green matter
1. C. 19 b.+f.....	12	1.16	10.37
2. C. 15.....	8.90	0.80	11.12
3. D. 20.....	14.90	1.14	13.07
4. C. 13.....	13.08	0.94	13.91
5. C. 7.....	15.65	0.98	15.96
6. C. 16.....	15.25	0.93	16.39
7. C. 19 (fungus).....	17.93	1.60	11.20
8. C. 17 (fungus).....	17.40	1.01	17.22
9. C. 9.....	18.07	1.06	17.04
10. C. 21 (fungus).....	27.33	2.36	11.58
11. Alder tubercles.....	50.31	2.20	22.86
12. Mixed culture of above....	67.48	1.92	35.14

Atmometer: 11.7 cc. daily average

ing in agreement with the several experiments which were conducted, that analyses with reference especially to the ratio between the carbon and nitrogen content of the plants are much to be desired. Experiments on the availability of nitrogen in peat have been made by a number of workers, but mostly upon sun-dry or

kiln-dry peat, the solubility of which in water is very low. The results confirm, however, both an increase in the production of dry matter in plants, and of dry matter relatively richer in the amount of nitrogen, as compared with the percentage in plants from soils lacking peat.<sup>9</sup>

Additional evidence of a similar nature is derived from experiments of more recent date with pure cultures of isolated bog organisms growing in sterilized solutions of bog water and peat (table IV, nos. 7 and 10), and from the preliminary work upon peat composted with the bacterial life from stable manure. They confirm the earlier experiments and also demonstrate the ability of some mycelial bog fungi and the organisms in alder tubercles<sup>10</sup> to increase transpiration and green weight of wheat plants about 200 per cent above that in untreated bog water. Normal appearance is here associated with a uniformly higher absorption of the solution, amount of transpiration, and green weight produced, and with the healthy condition of roots and leaves. The wheat plants in the cultures have the usual osmotic pressure isotonic with about a 0.2 to 0.3 normal potassium nitrate solution. Difficulty in absorption and tolerance or the xerophytism in bog plants do not seem to be correlated with high osmotic pressure.<sup>11</sup>

The point of most importance which should be noted in this connection is the obvious difference in the water requirements of the plants. Water and its solutes, whether organic compounds or inorganic salts, are as a general rule taken up in a different ratio from that existing in the substratum. The existing differences in the various colloids of cells would naturally tend toward inequalities in the amount of water or solutes absorbed and held by the tissues of the different varieties of species; the diosmotic properties of the protoplasmic membrane, differing according to the species

<sup>9</sup> HASKINS, H. D., The utilization of peat in agriculture. Massachusetts Sta. Rept., pt. 2:39-45. 1909.

LIPMAN, J. G., Report of the soil chemist and bacteriologist of the New Jersey Agricultural Experiment Station. 1910. pp. 188-195.

<sup>10</sup> SPRATT, E. R., The morphology of the root tubercles of *Alnus* and *Elaeagnus* and the polymorphism of the organism causing their formation. Ann. Botany 26: 119-128. 1912.

<sup>11</sup> FITTING, H., Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. Zeitschr. f. Bot. 3:209-275. 1911.

used as an indicator, would further determine the difference and variability in absorption, resistance, or tolerance. Inasmuch as the amount of mineral salts in bog soils and the amount used in the growth of bog plants is very small, and since the lack of larger quantities is not a factor in the succession of bog associations, the most fundamental distinction is that which controls the supply of available water. A method of determining the ratio between ash and the yield in organic compounds on the basis of the water requirement of plants for the period of their growth would have the merit of convenience, and, it must be admitted, the accuracy which is often questionable in the unit employed and as preferably expressed in agricultural literature. The unit of water requirement now used in agricultural texts for ten different economic species is 450 pounds of water for one pound of dry matter produced. Data of that character do not place the classification and comparison of soils, correlations with fertility or with age of plant, maximum growing period, and seasons on a measurable basis. The unit is numerically inaccurate and does not express the fundamental and causal relations.

Experiments upon the transpiration value of bog plants in relation to structure and habitat, to be published later, have shown that the data cannot always be expressed satisfactorily in the  $gm^2h$  system. Transpiration is a reciprocal relation. It is affected by the conditions which react upon the absorbing roots, and it is associated with chlorophyll activity and the absorption of carbon dioxide in the vertical gradient. Transpiration in the lower, more humid stratum of a bog meadow is often slight for days at a time. The luxuriousness of the vegetation and the amount of dry matter produced do not vary in this case with the transpiration quantity, but with protoplasmic permeability and the specific metabolism, permitting of exchanges by solubility, and with the active enzymic agents within the cells which effect the assimilation or the destruction of the substances in the external medium. Whatever the cause of the differential permeability,<sup>12</sup> solubility

<sup>12</sup> CZAPEK, F., Über eine Methode zur direkten Bestimmung der Oberflächenspannung der Plasmahaut von Pflanzenzellen. Jena. 1911.

LEPESCHKIN, W. W., Zur Kenntnis der chemischen Zusammensetzung der Plasmamembran. Ber. Deutsch. Bot. Gesells. 29: 247-260. 1911.

of the substances in the medium and in the plasmatic membrane is prerequisite to penetration (osmosis) into the living cells.

In previous publications on the factors by which the present bog vegetation is determined the writer pointed out that different species of cultivated plants show marked differences in the degree of sensitiveness to the toxic conditions of a bog habitat. That the stunted plants in these experiments have not lost their capacity for absorption and growth can be readily demonstrated. The plants resume their natural functions as soon as they are placed in dilutions less fatal in its effects. In contrasting the differences in physiological activity it was further shown that various phases of absorption and transpiration resulted from the progressive addition to the medium of chemically inert filtering materials. Types of soil were used ranging from the weathering products of soil-forming rocks to the completely oxidized products characteristic as the final residue. Incidentally it was shown that the normal growth of the plants in the uncontaminated soils was replaced by an abnormal retardation. In the main the study indicated that upon extraction of the injurious substances by means of insoluble adsorbing bodies, not only the differences between different species as to their tolerance and resistance were less pronounced, but also the differences in toxicity existing between the several zones within the same habitat. The selective action of the habitat was shown to be greatly diminished upon the removal of the injurious organic substances accumulating in the peat substratum. The conclusion was drawn that the relative power in bog plants for absorbing or rejecting the injurious constituents of bog soils and bog water was therefore the limiting factor, controlling the survival value of invading species and of plants native to the habitat. The roots of bog xerophytes are not much shorter than those of other plants; the lateral roots develop extensively, and the prevalent direction of root growth is horizontal rather than downward. This reaction cannot be regarded as one due to low soil temperature or to a slight oxygen content. The inhibitory factor for root growth which increases with depth is the reducing action of the substratum and the incomplete disintegration of organic compounds. It is now well known that certain root enzymes are oxidizing agents

which assist in the destruction of deleterious compounds in soils of an organic nature, and that the oxidizing action becomes lessened when the injurious organic substances are in excess. The wide variations in this functional reaction are probably of greater importance than external factors. It seems a tenable hypothesis, therefore, that the survival or the extinction of invaders may depend more upon the degree of functional plasticity than is generally admitted.

The experiments here cited furnish nothing more than an indication of the relative importance of some of the factors involved. The weight of evidence is obviously incomplete, for numerous important considerations have received no attention whatever in the present paper. The problem of absorption is not one of simple solution, but an intricate and coordinated process, and much needs to be known of the energy relations between plants and habitat and the organization of the protoplasmic membrane of absorbing organs. From the present study the following relations may be summarized:

1. Physiological investigations of peat soils have brought out clearly the fact that the character of the obligate bacterial flora and the nature of the organic compounds produced form a very important factor in the relative fertility of peat soils, in the causes of vegetation succession, in the distributional and genetic relationships of associations, and in the characteristic xeromorphy of both ancient and modern bog vegetation.

2. In view of the widely differing behavior of agricultural varieties in a bog water solution, and the interesting observation that the plants respond differently to the same solution, the conclusion is inevitable that here the source of the difference must logically be looked for not in the solution alone, but in the condition of the plants as well.

3. Since certain of the organic compounds eventually penetrate the protoplasmic membrane of absorbing organs and inhibit growth, it is evident that much importance must be ascribed to the influence exerted upon the plasmatic membrane, to the consequent differences in its diosmotic properties, and to the pathological changes induced which accompany the absorption of the injurious substances.

4. Some plants in contact with peat soil solutions may cause the organic constituents to be precipitated in an insoluble form.

5. In other plants the different organic carbon and nitrogen compounds arising in peat through the activity of microorganisms may be absorbed and assimilated. The chemical formula and transpiration data alone afford no indication of the physiological importance of the substances, hence the nutritive value of these compounds should be estimated on the basis of the total water requirement of a plant during its period of growth and the ratio between carbon, nitrogen, and ash in the plant.

6. The phenomena of absorption and tolerance of plants in bogs deal plainly not with osmotic pressure relations so much as with considerations of the permeability of the absorbing protoplasmic membrane, its power of endurance, and its ability by enzymic action either to absorb and assimilate or to transform injurious bodies into insoluble, impermeable compounds.

7. The organic disintegration substances in peat soils, while inhibitory to agricultural plants, have little or no effect upon certain xerophytic plants. It is concluded, therefore, that they may be positive forces not only in producing the natural succession of vegetation in bogs, but also in determinating xeromorphy and the associated relation of the members, within each group, which best succeed upon peat deposits. These organic substances play the differentiating rôle and are a cause of the infertility of peat deposits even when the amount of air and water in the soil is abundant and the temperature and humidity conditions are favorable to growth.

It is needless to point out that these facts have an important bearing on the agricultural exploitation of peat deposits and on the subject of the proper value of peat land to agriculture.

It is a pleasant duty to record my thanks to Mr. M. G. DICKEY and Mr. M. COROTIS for their assistance in obtaining the transpiration data in tables I to III.

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